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EFFECTS OF ROAD-STREAM CROSSINGS ON POPULATIONS OF THE IDAHO GIANT SALAMANDER (Dicamptodon aterrimus)

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EFFECTS OF ROAD-STREAM CROSSINGS ON POPULATIONS OF THE IDAHO GIANT SALAMANDER (*Dicamptodon aterrimus*)

By

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ABSTRACT

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EFFECTS OF ROAD-STREAM CROSSINGS ON POPULATIONS OF THE IDAHO GIANT SALAMANDER (*Dicamptodon aterrimus*)

Chairperson: Dr. Winsor H. Lowe

Habitat disturbances affect wildlife populations through numerous mechanisms, and determining specific components of habitat disturbances affecting those populations is challenging. For example, a single disturbance can both change local habitat conditions and impose limitations on dispersal of animals. Both of these components can negatively affect biological responses, such as body condition, local movement patterns, or survival. Culverts are a habitat disturbance having both of these components. Culverts affect local habitat conditions by increasing sediment levels in downstream reaches, negatively affecting animals downstream of culverts. Culverts also impose limits on dispersal by blocking passage of stream organisms to upstream reaches, negatively affecting populations upstream of culverts. Therefore, because the negative effects of the components of the habitat disturbance can be spatially separated (i.e., downstream v. upstream), we can determine which component may be responsible for negative trends attributed to culverts observed at the landscape scale. Road density and culverts have been negatively associated with occupancy of streams by *Dicamptodon aterrimus*, the Idaho giant salamander, but the underlying mechanism is unknown. I assessed the effects of road culverts on sediment levels and dispersal of *D. aterrimus* in nine streams. I then assessed the effects of culverts on three biological responses of *D. aterrimus*: body condition, in-reach movement behavior, and survival. I conducted my study in streams with three crossing types: unimproved culverts, improved culverts, and streams with no culverts. I predicted that changes to local habitat conditions downstream of culverts would negatively affect biological responses of individuals downstream of culverts. I predicted that limits on dispersal to reaches upstream of culverts would negatively affect biological responses in reaches upstream of culverts. I found no evidence culverts affected local habitat conditions, dispersal of *D. aterrimus*, or biological responses of *D. aterrimus*. Habitat disturbance from culverts might not affect *D. aterrimus* because this species is a habitat generalists and may not have responded biologically to the pressures of isolation. Though I did not find evidence that rates of upstream dispersal varied among crossing types, it is logical that unimproved culverts do block the upstream dispersal of aquatic *D. aterrimus* and reduction of these movements could have negative consequences in the long-term. Therefore, managers should aim to include stream amphibians in stream restoration goals.

Contents

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INTRODUCTION

Anthropogenic changes to ecosystems negatively affect species across taxa (Chapin et al. 2000). For example, declining trends in site occupancy, vital rates, and biodiversity have occurred due to pressures such as predation by introduced species (Kats and Ferrer 2003, Pilliod et al. 2010), climate change (Pounds et al. 2006), and especially habitat disturbance (Alford and Richards 1999). By the year 2100, habitat disturbance is expected to be the leading cause of declines in biodiversity (Sala et al. 2000). Habitat disturbance can negatively affect species through numerous mechanisms, including localized effects on habitat conditions (Beebee 1977, Corn and Bury 1989, Ash 1997) and disruption of dispersal among habitat patches (Marsh et al. 2005, Fahrig 2007, Shepard et al. 2008). These mechanisms can impact the fitness of individuals by affecting biological responses such as body condition (Burton et al. 2006), local patterns of movement (Clobert et al. 2009), and survival (Saccheri et al. 1998). However, disentangling how habitat disturbances mechanistically affect wildlife populations and, likewise, determining which specific components of habitat disturbance drive trends of wildlife populations has been a challenge for ecologists (Fahrig 2003).

Culverts are a ubiquitous form of human mediated habitat disturbance in stream systems, affecting wildlife populations by changing local habitat conditions (Rice 1999, LeMoine 2007) and limiting movements along stream channels (Warren and Pardew 1998). Effects of these components of habitat disturbance from culverts are spatially separate in stream systems. Culverts affect local habitat conditions in streams by increasing sedimentation downstream of culverts (Clarke and Scruton 1997, Rice 1999), which can negatively affect vertebrates through both indirect effects that cascade through food webs (Henley et al. 2000) and direct effects on vital rates (Newcombe and Macdonald 1991). Culverts also limit upstream movements of animals (Gibson et al. 2005, Foster and Keller 2011) by forming impassable reaches due to perched outlets (Park et al. 2008) and amplified water velocities within culverts (Warren and Pardew 1998). Limits to upstream movements by culverts could limit dispersal to upstream reaches, thereby reducing the potential for immigrants to reach populations above culverts. Barriers to migrants among populations can lead to genetic isolation of populations (Keller and Largiader 2003, Wofford et al. 2005, Epps et al. 2005), which can lead to inbreeding depression and population declines (Madsen et al. 1996, Westemeier et al. 1998). Interestingly, because the

effects of the components of habitat disturbance caused by culverts can be spatially separated at the local-scale (i.e., increased sedimentation will negatively affect populations downstream of culverts, barriers to dispersal will negatively affect populations upstream), we can determine which component may be responsible for negative trends attributed to culverts observed at the landscape scale.

Presently, land managers in the United States are working to improve many culverts by limiting their negative effects on local habitat conditions and allowing animals unrestricted movement along stream corridors, but much of this work has focused on fish. Culvert improvements generally include building natural stream bottom throughout the length of culverts, setting gradients of culverts similar to the gradients of the streams they bisect while setting the outlets of culverts at stream grade, and building culverts wider than the wetted width of streams during base flow. Unimproved culverts generally do not have natural substrate throughout the length of the culvert, are often narrower than the wetted width of streams during base flow, and generally have perched outlets that are above the grade of the streams. Henceforth, I categorize culverts under these two types: (1) improved and (2) unimproved. Most culvert improvements are targeted towards restoring habitat and passage for fish, and in particular salmonids. Likewise, most research regarding the efficacy of culvert improvements for restoring passage for aquatic species has also focused on fish. Meanwhile, little research has focused on how these structures affect the movements of other aquatic species (but see, Sagar et al. 2007, Foster and Keller 2011). To my knowledge, no stream culvert has been improved with the specific intent of allowing the unimpeded passage of other taxa, such as stream amphibians or invertebrates.

Stream amphibians are a group of organisms likely affected by the two components of habitat disturbances caused by culverts (Sagar et al. 2007, Ward et al. 2008). For example, the abundance, diversity, and richness of stream salamanders in West Virginia have been affected by changes to habitat conditions attributed to culverts (Ward et al. 2008). Specifically, because poorly constructed culverts can lead to increased sedimentation in reaches downstream of these structures (Clarke and Scruton 1997, Rice 1999), stream amphibians – whose fitness may be sensitive to sediment level (Lowe et al. 2004) – may be negatively affected by increases in

sediment caused by culverts. High sediment loads can also reduce growth of amphibian larvae (Gillespie 2002) and reduce density of stream salamanders (Corn and Bury 1989).

The second component of habitat disturbance from culverts that likely affects stream amphibians is potential blockage of upstream dispersal (Lowe 2003). These events are important for maintaining connectivity among populations of aquatic animals occupying headwater streams, because downstream reaches are likely the primary source of immigrants to these populations. If this source of immigrants is blocked by an unimproved culvert, populations in upstream reaches will not have the benefit of genetic rescue, which can be important for long-term viability of populations (Wright 1949). Immigration reduces the threat of genetic drift and inbreeding, which can result in reduced fitness for individuals (Keller 1998, Slate et al. 2000). However, even a single migrant per generation can maintain enough genetic connectivity between populations to prevent negative effects of drift and inbreeding in small isolated populations, though as many ten migrants may be needed in some populations (Mills and Allendorf 1996).

Dicamptodon aterrimus, the Idaho giant salamander, inhabits headwater streams in northeastern Idaho and extreme western Montana (Stebbins 2003), and may be particularly affected by culverts through changes to habitat conditions or limits on dispersal (Sepulveda and Lowe 2009). *D. aterrimus* are facultatively paedomorphic (Cope 1889, Nussbaum 1976), meaning individuals may be reproductively mature as aquatic larval-like forms that retain gills for life, or as terrestrial adults. Hence, *D. aterrimus* are capable of moving within streams or over land, though molecular evidence indicates dispersal primarily occurs along stream corridors (Mullen et al. 2010). There are high densities of roads and streams in the range of *D. aterrimus*, resulting in high numbers of culverts. Land management agencies have improved many culverts in this range; however, many unimproved culverts remain that could affect local habitat conditions and dispersal of *D. aterrimus*. These local effects from unimproved culverts could be driving a trend of decreased occupancy associated with road density for this species (Sepulveda and Lowe 2009). Specifically, culverts could impact *D. aterrimus* populations through at least two mechanisms. First, culverts could impact local habitat conditions important to *D. aterrimus* downstream of culverts, such as by increasing sediment loads. Second, because *D. aterrimus* primarily disperse

along stream corridors, culverts could limit *D. aterrimus* dispersal events to reaches upstream of culverts.

I hypothesized that habitat disturbance from culverts would drive local habitat changes in streams and limit dispersal of *D. aterrimus* to reaches upstream of culverts, resulting in decreased body condition, changes to in-reach movement behaviors, and reduced survival of *D. aterrimus*. To test these predictions, my goals were: (1) to determine if culverts are barriers to dispersal of *D. aterrimus* to reaches upstream of culverts; (2) to determine if local habitat conditions are affected by culverts; and (3) to determine if variation in body condition, survival, or in-reach movement behaviors, if present, was more likely influenced by changes in local habitat conditions or limits to dispersal. To accomplish these goals, I conducted capture-mark-recapture (CMR) surveys in nine streams with three replicates of each of three crossing types: (1) streams bisected by unimproved culverts, (2) streams bisected by improved culverts, and (3) reference streams, which were not bisected by either type of culvert nor crossed by a roadway.

Specifically, I predicted that habitat disturbance from unimproved culverts, and to lesser extent improved culverts, would increase sediment in streams below culverts, in turn negatively affecting body condition, in-reach movements, and survival of *D. aterrimus* in reaches downstream of these structures. I also predicted that unimproved culverts would impede dispersal of *D. aterrimus* from downstream to upstream reaches, where I defined dispersal as permanent movement from one reach to another. I predicted that, in turn, these limits to dispersal would negatively affect body condition, in-reach movements, and survival of *D. aterrimus* residing in reaches upstream of unimproved culverts. I also predicted that improved culverts would not impede the upstream dispersal of *D. aterrimus*. However, because these structures were only recently replaced, I predicted that limits to dispersal prior to improvement may have continued to influence biological responses because it can take multiple generations for genetic rescue effects to be detectable in fitness traits (Bryant et al. 1999)

METHODS

Species and System

D. aterrimus inhabit headwater streams within mountainous portions of northeastern Idaho and extreme western Montana (Stebbins 2003). The northern extent of *D. aterrimus* is approximately delineated by US Interstate 90. Their range extends south through the Saint Joe and Clearwater River drainages to its southernmost extent in the South Fork of the Salmon River (Carstens et al. 2005). In Montana, *D. aterrimus* are found within several streams of the Saint Regis River basin in Mineral County. Congeners of *D. aterrimus* occur in areas along the Pacific Coast of North America that are spatially isolated from the range of *D. aterrimus*. Orogeny of the Cascades and subsequent desertification of the Columbia basin during the Pliocene is thought to have separated *D. aterrimus* from the Pacific Coast *Dicamptodon* species (Steele et al. 2005). Therefore, *D. aterrimus* is an isolated species.

D. aterrimus primarily inhabit headwater streams, but also occur in higher order streams and rivers and can be found in headwater lakes. Within stream corridors, individuals are found in pools and under rocks and logs. Based on findings in *D. tenebrosus*, *D. aterrimus* might also occur within the hyporheic zone, a transitional region between the substrate of streams and ground water below (Feral et al. 2005). Also, during culvert replacements, congregations of *D. tenebrosus* and *D. aterrimus* have been discovered residing under culverts (Fellers et al. 2010). Therefore, it is likely that *D. aterrimus* individuals can remain beneath the substrate, including man-made structures, for extended periods of time. *D. aterrimus* are robust salamanders measuring up to 220 mm snout-vent length (SVL) and have a stout, streamlined body. They feed on invertebrates, small fish, small mammals, larvae of Rocky Mountain tailed frogs (*Ascaphus montanus*), and conspecifics. *D. aterrimus* may compete with salmonids and sculpin for prey items (Metter 1963, Petranka 1998).

Because *D. aterrimus* are facultatively paedomorphic, adults can exist as either paedomorphic or terrestrial forms. The terrestrial form is thought to be less common than the paedomorphic form; however, knowledge of the ratio of adult morphs may be skewed because most surveys have occurred within and along stream corridors. Because of this dimorphic life history, *D. aterrimus* have two potential movement pathways: (1) movements within the stream corridor by larvae,

paedomorphs, and terrestrial forms, and (2) movements overland by terrestrial adults. In-stream movements of less than 50 m are common for paedomorphs and larvae, but longer movements have been recorded (Sepulveda and Lowe 2011). In a pair of streams, Sepulveda and Lowe (2011) found that *D. aterrimus* in-stream movements varied with individual size, where individuals that moved upstream were on average larger than individuals that moved downstream. Direct measurements of movements by terrestrial morphs of *D. aterrimus* are lacking. However, information from 35 radio tagged *D. tenebrosus* individuals indicates that terrestrial morphs average up to 10 m of movement per day (Johnston and Frid 2002). Despite the two potential movement pathways, genetic evidence suggests *D. aterrimus* primarily disperse along stream corridors (Mullen et al. 2010).

D. aterrimus are distributed patchily throughout their range (Petranka 1998). Sepulveda and Lowe (2009) showed that this distribution was explained, in part, by landscape-level patterns of logging history, road density, and forest structure. The in-stream habitat variable that best explained *D. aterrimus* density was amount of embedded substrate, where – surprisingly – amount of embedded substrate was positively correlated with *D. aterrimus* density. Their models also suggested that streams without fish contained higher densities of *D. aterrimus* than streams containing fish.

I conducted my study in streams located in the Lochsa, Saint Joe, and Saint Regis river basins (Figure 1). To account for spatial variation, I considered the three basins to be within two geographic regions of my study area: the northern and southern regions. The northern region included the Saint Joe and Saint Regis because these basins share a watershed boundary. The Lochsa is spatially separated from the Saint Joe and Saint Regis basins, so I considered streams within this basin ($n = 5$) to be within the southern region. Both regions are dominated by mixed conifer forests. There has been a long history of logging activity and road building in both regions, and lands are a mix of private and United States Forest Service (USFS) ownership. However, all of my study streams were on USFS land. *D. aterrimus* share many streams in these areas with fishes.

Study Design

To assess the effects of road crossings on the body condition, in-reach movement behavior, and survival of *D. aterrimus*, I conducted CMR surveys in nine streams representing three crossing types. Three of these streams were bisected by unimproved culverts, three streams were bisected by improved culverts, and three streams served as reference streams, which were not bisected by either type of culvert (I further define these culvert types in the next section). In each stream bisected by a culvert, I surveyed 80 m reaches directly above and below each culvert. In each of the reference streams, I established the downstream and upstream survey reaches separated by a 20 m "dummy" reach; twenty meters was the mean length of the culverts in the six streams with culverts.

From this point forward, I use the following terms to describe my study system. I use the term "intervening reach" to collectively refer to the stream section between the upstream and downstream study reaches for all crossing types. I define a "reach" as a continuous segment of stream that is wholly above or wholly below the intervening reach. I use the term "stream" to encompass the pair of study reaches on one stream, separated by the intervening reach. I refer to the "downstream reach" as the reach below the intervening reach in a stream, and I refer to the "upstream reach" as the reach above the intervening reach in a stream. I refer to "reach position" as a binary factor describing the downstream or upstream position of reaches within streams.

In all analyses, I considered the crossing type (reference, improved culvert, unimproved culvert) and reach position (downstream or upstream) as categorical factors, where reach position was nested within stream. I also used a binary factor of road presence to differentiate streams crossed by either culvert type – improved or unimproved – from the reference streams. I considered stream a random variable to control for variability among streams.

I selected my nine study streams based on information from abundance surveys of *D. aterrimus* and qualitative assessments of culverts (see Appendix 1 and 2). Briefly, I chose study streams with relatively high abundances of *D. aterrimus* and with culverts that best fit the definitions of unimproved and improved culverts.

I expected there to be variation in geomorphology and stream habitat between streams with improved and unimproved culverts because the USFS prioritizes culvert replacement to maximize stream access and habitat patch size for fish. Prioritized locations for culvert improvements are lower in watersheds where streams are wide, slopes are gentle, and fish are likely to be present. Culverts are not prioritized when relatively high in watersheds, when streams are relatively narrow, steep, and less likely to contain fish, and when culvert replacements would open up relatively little stream area to fish. Therefore, it was logistically difficult to choose study streams with improved and unimproved culverts where geomorphology and stream habitat were similar.

Habitat Measurements

I quantified variation in several local-scale habitat parameters among streams. Specifically, I measured local-scale habitat variables that could directly or indirectly affect *D. aterrimus* (Sepulveda and Lowe 2009) or that could bias results of the study. I measured percent fine sediment because it has often been negatively associated with stream health and abundance of stream salamanders (Waters 1995, Welsh and Ollivier 1998, Lowe et al. 2004), although Sepulveda & Lowe (2009) found that fine sediment was positively associated with *D. aterrimus* density. I also measured habitat variables that might affect percent fine sediment, survey effort, estimation of survival, or aspects of movement behavior. These variables included bankfull width, wetted width, water depth at the thalweg, percent of pool habitat, and stream gradient.

Other than stream gradient, I measured habitat variables in one-meter long transects. The widths of these transects were delineated by the wetted width of the stream. I randomly placed transects within each 10 m of channel length in each study reach, resulting in eight habitat transects per study reach. I estimated percent fine sediment within each transect by estimating the percent of area within the transect that was covered with particles less than two millimeters in diameter (Lane 1947). I measured bankfull width as the distance between the banks of the channel at peak flow, as determined by a change in slope or vegetation along the stream bank. I measured wetted width and water depth at base flows at the end of August. I determined the percent of pool habitat in each transect by estimating the area of the water surface that was pool. I measured

stream gradient, in degrees, along a 10 m stream section, where the mid-point was the lower end of the one-meter habitat transect.

CMR Survey Sessions

To assess survival and movement of *D. aterrimus*, I conducted CMR surveys in the nine study streams. At eight of these streams, I conducted surveys during three primary survey periods in 2012 and 2013. At one stream, Float Creek, I conducted surveys during two primary periods in 2012 and during three primary periods in 2013. Within each primary period in 2012, I conducted either two or three surveys. Within each primary period in 2013, I conducted two surveys. In 2012, I conducted surveys between June 20 and September 9. In 2013, I conducted surveys between June 30 and September 4. Within primary survey periods, intervals between secondary surveys ranged from one to seven days. Intervals between primary periods within years ranged from 14 to 27 days.

During the first primary survey period at each stream, I surveyed the first 50 m of the 80 m-long reaches contiguously adjoining the intervening reaches. In order to recapture individuals that may have emigrated from these initial 50 m of stream, I extended the edges of each downstream and upstream reach 10 m in each of the second, third, and forth primary survey periods. That is, during the second, third, and forth primary period surveys the downstream and upstream reaches were 60, 70, and 80 m in length, respectively. I maintained reach lengths at 80 m for the fifth and sixth primary periods. I also marked all new salamanders I encountered in these extended sections.

For all but two surveys, streams were surveyed by a three-observer crew (on one occasion there were two observers and on one occasion there was only one observer). The first observer wielded a Smith-Root LR-24 backpack electrofishing unit. The second observer wielded a dip net and worked alongside the first observer to capture stunned *D. aterrimus* or chase *D. aterrimus* that alerted to the electric current or the observers. The third observer wielded a seine net and worked approximately 1 m downstream of the first observer to capture individuals stunned and drifting in the current, or attempting to evade capture by swimming downstream. I also noted fish species present during surveys.

Upon capture, I placed salamanders in individual plastic bags with water and recorded each individual's location along the study reach (+/- 1 m). During processing, individuals were kept inside their bags and kept cool by placing the bags in five gallon buckets of stream water. Individuals that had not been previously marked were anesthetized with approximately 150 mg/L solution of MS-222 or a 0.025 mL/L solution of benzocaine. I then assigned these individuals unique marks using visible implantable elastomer (VIE; Northwest Marine Technologies, Shaw Island, WA, USA). I photographed each individual on a stage, along with a measuring tape to allow for standardized measurements of body size. I recorded each individual's mass and SVL in the field. Digital photos were used to confirm field measurements of SVL. Finally, I examined the VIE marks of recaptures. To limit misreading of VIE marks by field observers, the marks of each individual were determined by two observers with normal color vision under an ultra-violet light. Further, to ensure that I assigned the correct marking pattern to the correct individual, VIE marks were cross-checked before release. Once all anesthetized individuals had regained full mobility, I released them back into the stream at their exact point of capture. Because correctly assigning, determining, and recording VIE mark patterns on individuals can be affected by observer error (Grant 2008), I used comparisons of photographs and repeated measures of SVL and mass between captures to exclude potentially erroneous capture records from my analysis.

Crossing type candidate model set

I built a candidate model set to test if changes to local habitat conditions or limits on dispersal caused by crossing types and road presence negatively affected the biological responses of body condition, in-reach movement behaviors, and survival of *D. aterrimus*. I also used this model set to test for the effects of crossing types and road presence on sediment loads.
I included the following four models in this set.

(1) I included a model with an interaction term of road presence × reach position to test if changes to local habitat conditions or limits on dispersal caused by culverts – whether improved or unimproved – affected the biological responses. This model structure tested two predictions. (a) I predicted that if changes to local habitat conditions caused by culverts – whether improved or unimproved – affected the responses, biological responses in reaches downstream of culverts would be different than those from all other stream reaches. This would suggest that impacts

from changes to local habitat conditions by unimproved culverts were similar to those from improved culverts. Changes to local habitat conditions that could negatively affect biological responses include effects on sediment loads, but also include possible unmeasured habitat changes. (b) I predicted that if limits to dispersal caused by culverts – whether improved or unimproved – negatively affected the responses, biological responses in reaches upstream of culverts would be different than those from all other stream reaches. This would suggest that impacts from limits on dispersal by unimproved culverts were similar to those from improved culverts. However, because the improved culverts in my study were only recently constructed to replace unimproved culverts, residual effects from past unimproved culverts could be partially responsible for the responses from streams with improved culverts.

(2) I included a model with an interaction term of crossing type × reach position to test if changes to local habitat conditions or limits on dispersal caused by unimproved culverts negatively affected the biological responses. This model structure tested two predictions. (a) I predicted that if changes to local habitat conditions caused by unimproved culverts negatively affected the responses, biological responses in reaches downstream of unimproved culverts would be lower than those from all other stream reaches. Changes to local habitat conditions that could negatively affect biological responses include effects on sediment loads, but also include possible unmeasured habitat changes. (b) I predicted that if limits to dispersal caused by unimproved culverts negatively affected the biological responses, biological responses in reaches upstream of unimproved culverts would be lower than those from all other reach types.

(3) I used a model including road presence to test if changes to local habitat conditions and limits on dispersal caused by culverts – whether improved or unimproved – negatively affected the biological responses. This model structure tested the prediction that if culverts limited dispersal to upstream reaches and caused changes to habitat in downstream reaches that negatively affect the biological responses of *D. aterrimus*, biological responses would be lower in streams with culverts than in the reference streams.

(4) I used a model including crossing type to test if changes to local habitat conditions and limits on dispersal caused by crossing types negatively affected the biological responses. This model

structure tested the prediction that if improved or unimproved culverts limited dispersal to upstream reaches and caused changes to habitat in downstream reaches that negatively affect the biological responses of *D. aterrimus*, biological responses would differ among crossing types.

Statistical Analysis: Habitat, Body Condition, In-reach Movement

I used a two-step model selection process to determine the effects of crossing types and road presence on stream sediment and biological responses of *D. aterrimus*. During the first step I determined the most parsimonious structure of habitat and biotic conditions to explain each response. Below I refer to the structure resulting from this first step as the "habitat/biotic structure." The habitat conditions I modeled in the first step included abiotic variables (percent pool, wetted width, stream gradient, percent fine sediments), biotic variables (fish presence, SVL of *D. aterrimus* individuals), and the region in which the stream was located (north or south). This list was compiled based on previous studies and includes all variables used in the analyses of sediment, body condition, and in-reach movement. Therefore, each analysis did not contain each variable, and each candidate set of models was different. In each candidate model set I included a model with only random intercept effects of stream. For modeling the effects of crossing types and roads on sediment, this two-step process served to first account for habitat differences among the reaches that could affect sediment loads, prior to assessing the effects of the culverts themselves on sediment. For modeling biological responses, this process allowed me to first account for habitat differences among the reaches that could affect the biological response, prior to assessing the effects of the culverts themselves on the response. This process carries a similar logic to modeling survival from CMR studies, where the most parsimonious structure of capture probability is often determined before modeling survival (Lebreton et al. 1992). During the second step I incorporated the highest ranking habitat/biotic structure into the crossing type candidate model set described above.

I analyzed habitat, body condition, and movement responses in R (R Core Team 2014). I fit normally distributed mixed-effects models using the lme function in package nlme (Pinheiro et al. 2014), binomial distributed mixed-effects models using the glmer function in package lme4 (Bates et al. 2014), and beta distributed mixed-effects models using the glmmadmb function in package glmmADMB (Fournier et al. 2012, Skaug et al. 2013). For all model selection, I used

Akaike information criterion corrected for small sample sizes (AIC_c) with likelihood values estimated from maximum likelihood procedures (Burnham and Anderson 2002, Zuur et al. 2009). I considered models with Δ $AIC_c \leq 2$ to be competing models. For normally distributed models, I used restricted maximum likelihood procedures to estimate parameter values from the final models (Zuur et al. 2009). For selection of the top models in each step, I evaluated whether 95% confidence intervals for the parameter coefficients in competing models overlapped 0. I considered models containing parameter coefficients overlapping zero to be less informative than models containing parameter coefficients that did not overlap 0. In all models, stream was included as a random intercept variable. The fits of the final models were validated with plots of residual values against fitted values.

Habitat

I assessed two aspects of habitat variation. First, I assessed expected differences in geomorphology and stream habitat that exist among the crossing types due to the constraints of selecting streams with unimproved and improved culverts. Here I assessed variation in wetted width, stream gradient, and percent of pool habitat. Second, I determined the best model structure from the crossing type model set to explain variation in fine sediments. In both habitat analyses, I assumed a beta distributed variance structure to model response variables of sediment, pool coverage, and gradient, which were proportions (Ferrari and Cribari-Neto 2004). Because calculations under the beta distribution do not accept values of 0 or 1, these values were adjusted by adding or subtracting 0.01, respectively. Because recorded values of sediment and pool coverage were estimated visually, precision was relatively low, making this adjustment negligible.

Because I expected there to be differences in geomorphology and stream habitat that exist among the crossing types due to the constraints of selecting streams with unimproved and improved culverts, I assessed if the wetted width, stream gradient, or percent of pool habitat in streams varied by crossing type. For each metric I compared a model containing crossing type to a null model using a likelihood ratio test under a χ^2 distribution. I used maximum likelihood to estimate likelihood values. For all models I included stream as a random variable. To assess wetted width I used a linear mixed model with the natural log transformation of wetted width to meet

normality assumptions. To assess variation in gradient among crossing types, I modeled gradient as a proportion by dividing values of degrees by 360.

I used a two-step selection process to model how fine sediments were affected by crossing type. I included wetted width, stream gradient, percent pool, and region as possible parameters in the habitat/biotic model structure. These are habitat variables that can affect the amount of fine sediments in streams. Accounting for these variables allowed me to focus on the true effects of culverts on sediment loads, despite potential differences in other variables that can influence sediment. I then incorporated the highest ranking habitat/biotic model structure with the crossing type model structures. I log transformed wetted width, stream gradient, and percent pool to normalize their distributions. For percent pool, values of 0 and 1 were adjusted by adding or subtracting 0.01, respectively. I did not use bankfull width or stream depth because both terms were strongly correlated with wetted width (Graham 2003).

Body Condition

I used the scaled mass index (SMI) (Peig and Green 2009) to determine the best structure from the crossing type candidate model set to explain the body condition of *D. aterrimus*. The SMI allows for comparison of body condition among individuals from different populations and among individuals of different size classes. To assess body condition, I included individuals captured during all CMR surveys. When individuals were captured more than once, only the measurements from the initial capture were included. I excluded individuals from the analysis of SMI whose recorded masses and lengths I considered erroneous (Ellison and Gotelli 2004). To identify these cases, I regressed the natural log of mass on the natural log of SVL (n = 963). I then flagged cases outside of the 99% prediction interval from the model as suspect of measurement error. I also regressed mass on SVL, without transformation, and flagged cases that appeared to lie outside the standard scatter of the plot. For flagged cases, I then examined digital photographs of the individuals in Image J (Schneider et al. 2012) to confirm the field measurements of SVL. For cases in which a field measurement error of SVL was evident, I replaced the field data with the new measurement obtained from Image J measurement. I then regressed the natural log of mass on the natural log of SVL again and removed from the SMI

analysis cases outside the 99.9% prediction intervals from the model. I used the remaining cases (n = 950) to model SMI.

For modeling salamander body condition, I included biological variables of fish presence and individual salamander SVL in the habitat/biotic structure. Abiotic variables included percent pool, percent fine sediments, stream width, and region. For each of these abiotic variables, I used the mean value from each reach for input to the models and, therefore, transformations of these variables were not necessary. I included models with interactions and additive terms in the habitat/biotic candidate model set. Because the size range of individuals differed between regions (north v. south), I used an interaction term of SVL × region. I included an interaction term of fish × SVL because fish might affect different sized salamanders differently (Lowe et al. 2004). Fine sediments can affect biological responses of salamanders (Corn and Bury 1989), and might differentially alter behaviors that influence the growth of individuals depending on salamander size (Lowe et al. 2004). Therefore, I included a three-way interaction of SVL × percent fine sediments × fish. I had *a priori* predictions that patterns of sediment loads would be inherent to culvert types and reach positions. Had these predictions held, I would not have needed to account for differences in sediment in these models. However, because my habitat analysis indicated that culverts did not affect sediment loads, I included the effects of sediment in the habitat/biotic portion of model selection, rather than allow difference in sediment to be absorbed by the crossing type model structures. In the second stage, I incorporated the highest ranking habitat/biotic model structure with the crossing type model structures. To account for increasing variance in the residuals plotted against the fitted values of the full model (Zuur et al. 2009), I used 1/SVL for a weighted variance structure.

In fish, the body conditions of individuals with relatively high growth rates are often relatively lower compared to individuals with lower rates of growth (Bolger and Connolly 1989), and this could be a pattern in salamanders as well. I tested for this pattern in *D. aterrimus* using individuals initially captured in 2012 and subsequently recaptured in 2013. For each individual, I used the difference between the initial and final SVL measurements and divided this value by the number of days between those captures, which provided the average daily growth rate. I used simple linear regression to model the relationship.

Movement

I analyzed two aspects of in-reach movement behavior of *D. aterrimus*: whether an individual moved or stayed and whether an individual moved in an upstream or downstream direction. I used net movement to quantify these response variables. I defined net movement as the difference between the locations of the initial and final captures. In these analyses, I included all individuals that were recaptured at least once.

Because factors influencing movement behavior may vary among the aspect of movement in question, I allowed the habitat/biotic model structure to vary among tests. However, I began model selection for each aspect of movement behavior with the same candidate set of models. In these models, I included an interaction between individual size and fish presence because the presence of fish might affect the tendency for *D. aterrimus* to move (Barr and Babbitt 2007, Leuthold et al. 2012) and this response might vary depending on *D. aterrimus* size. I included stream gradient because steeper gradients might affect the movement of salamanders differently than shallow gradients. I used the ratio of residual deviance (resid. dev.) to residual degrees of freedom (rdf) to check for overdispersion of logistic regression models fit to the binomial distribution. Once I established the structure of the habitat parameters for each aspect of movement behavior, I then tested for model fit of the crossing type model structures.

I used logistic regression to assess fit of the crossing type model structures for explaining whether individuals moved or stayed. I defined individuals that moved as those with net movements of greater than 1 m in an upstream or downstream direction. I defined individuals that stayed as those with absolute net movements of less than or equal to 1 m. I also used logistic regression to determine the best structure from the crossing type model set to explain if individuals were likely to move upstream or downstream. I defined individuals that moved upstream and downstream as those individuals with net movements greater than 1 m in an upstream or downstream direction, respectively.

An initial goal of this project was to test for variation among crossing types in the frequency *D. aterrimus* disperse between reaches, but these events were rare. Within all 9 study streams, I detected a total of 15 individuals that dispersed between reaches within streams. In all cases the

individuals dispersed from the upstream reach to the downstream reach. Eleven of those events occurred in Bird 1, two occurred in Badger, and one was in each of Float, Pagoda, and Mayo. Because the majority of these individuals were located in a single stream, I did not have power to compare the probabilities of movement between reaches among the crossing types using a multistate model in program MARK (White and Burnham 1999).

Statistical Analysis: Survival

To determine the best structure from the crossing type candidate model set to explain differences in apparent survival of *D. aterrimus*, I modeled my CMR data in program MARK using the Cormack-Jolly-Seber (CJS) framework (Cormack 1964, Jolly 1965, Seber 1965). I originally designed the temporal layout of my surveys to work in the framework of Pollock's robust design (Pollock 1982). However, I was not able to fully parameterize the temporary migration parameters of this model or of a multistate model (see movement methods). Therefore, I collapsed the survey sessions in each primary period into a single occasion. To assess the survival of individuals that dispersed between reaches, a multistate model would be necessary. Therefore, I removed from the survival analysis the 15 individuals that dispersed from upstream to downstream reaches because their survival depended on conditions of both reaches.

CJS models are parameterized by apparent survival and recapture probability. Because apparent survival was my parameter of interest, I first used model selection to determine a parsimonious structure of recapture probability (Lebreton et al. 1992), while retaining a consistent structure of apparent survival. Because assessing variation of survival over time was not a priority, I allowed apparent survival to vary only by reach (n = 18) in these initial models. This represented the most general model of interest in my study. A test for goodness of fit using program Release in program MARK indicated I lacked power to detect a lack of fit (Test 2 + Test 3: df = 72, p = 1.0). Therefore, I did not adjust for overdispersion, leaving $\hat{c}$ = 1, and I assessed the structure of recapture probability within program MARK using AIC_c. Because the time intervals between my survey periods varied among streams, I used a weighted average of the interval lengths between time periods from all streams. I weighted this average by the cumulative number of individuals released from each stream prior to the survival interval, so that time intervals from streams with

more releases carried more weight in averaging. I used monthly survival (30.44 days) as my time-length of interest.

I found the most parsimonious structure for capture probability by including the following terms in model selection. Because I observed qualitative habitat heterogeneity among reaches that might result in differences in recapture probability, I allowed recapture probability to vary by reach and stream. Because I used an active capture method, rather than a passive trapping method, recapture probability was likely influenced by observer skill and alertness and may have varied over time. Therefore, I included time variation in models of recapture probability. Further, time variation allows for variation in recapture probability due to other unmeasured stochastic variables. Because captures from electrofishing are often biased by individual size, where larger individuals have a higher probability of recapture (Anderson 1995, Burgess 2001, Leuthold 2003), I included SVL at initial capture as an individual covariate. To determine if effort affected recapture probability, I used effort as a primary period specific covariate in these models. Because the widths and lengths of my study reaches varied (naturally and due to the sampling design, respectively), I standardized effort for each reach by dividing the search time by the estimated search area for each survey, where estimated search area was the length of the survey in meters multiplied by the mean wetted width of the reach (sec/m^2). Finally, because individuals near the ends of reaches may have been more likely to leave the reach and, therefore, less likely to be recaptured (Albanese et al. 2003), I included the distance of each individual's initial capture location from the lower end of the reach as an individual covariate.

Once I determined the most parsimonious model structure for recapture probability, I used Bayesian mixed-effects models executed in program MARK to answer questions regarding variation in apparent survival among the study reaches. I used this method because it allows for the experimental unit of reach to be treated as a random variable, thus avoiding problems with pseudo-replication that arise from pooling data across replicates (Schwarz 2002). Further, with this method it is possible to model a single posterior distribution and mean survival from multiple replicates. I considered reach the replicate level in this analysis and treated each reach as independent. Therefore, this analysis does not account for non-independence of the downstream and upstream reaches in streams.

The Bayesian mixed-effects models I executed in program MARK did not provide parameter estimates of interactive effects between road presence × reach position and crossing type × reach position, *per se*. Therefore, for each prediction of the crossing type model set, I developed a hyperdistribution. Within program MARK, Bayesian mixed-effects models are implemented by assigning replicates to hyperdistributions. Each hyperdistribution provides an estimate of mean apparent survival and a credible interval for the treatment of interest. For example, in my study the three reaches above unimproved culverts are three replicates that are included in a hyperdistribution estimating mean apparent survival of individuals in reaches above unimproved culverts. Using this method I obtained an estimate of mean apparent survival for each of the following treatment levels: reaches above roads, below roads, above unimproved culverts, below unimproved culverts, above improved culverts, below improved culverts, above the intervening reach in reference streams, below the intervening reach in reference streams, in reference streams, in streams with unimproved culverts, and in streams with improved culverts.

For each of the above hyperdistributions, I ran 5 MCMC chains, each with a tuning period of 4000 iterations, a burn-in period of 5000 iterations, and 20,000 iterations saved to file. I used the default non-informative priors in program MARK. I used the Gelman-Rubin test for chain convergence using the scale reduction factor (Gelman and Rubin 1992).

RESULTS

I captured 1,014 individual *D. aterrimus* across the nine study streams, including 977 paedomorphs and immature larvae and 37 terrestrial individuals. I excluded the terrestrial individuals from analyses because their biology differs fundamentally from the biology of the aquatic morph. Also, I captured relatively few terrestrial individuals compared to the aquatic morph and, therefore, did not have enough replicates to include morph as a factor in the analysis.

Habitat

Streams with improved culverts were wider than streams with unimproved culverts and no culverts (χ^2= 10.77, df = 2, $p < 0.01$). The widths of streams with unimproved culverts and no culverts were similar. The gradients of streams varied among the crossing types (χ^2 = 45.70, df = 2, $p < 0.01$). Streams with unimproved culverts were steepest, then no culverts, then improved

culverts. Streams with improved culverts had less pool habitat than streams with no culverts and unimproved culverts ($\chi^2 = 7.30$, df = 2, $p = 0.03$), which had similar amounts of pool habitat.

AIC_c indicated two habitat models shared nearly equal weight for explaining fine sediments. These models both included additive terms for region and percent of pool cover. They differed by the inclusion of an additive term for wetted width. Because 95% confidence intervals for the coefficient of wetted width overlapped 0, I selected the model lacking this term as the top habitat model (Table 1). After accounting for differences between regions and percent of pool cover, no model from the crossing type candidate model set improved fit (Table 2). Though the models including road and crossing type had Δ $AIC_c < 2$, 95% confidence intervals for all coefficients for crossing type candidate model set terms overlapped 0.

Body Condition

The most parsimonious structure of the habitat/biotic parameters for explaining variation in body condition included the interaction term SVL × percent fine sediments × fish presence (coefficient 95% CI: 0.05 - 0.13), along with an additive term for region (coefficient 95% CI: 0.41 - 0.85) (Table 3). Dropping either of these terms from model structures resulted in AIC_c weights < 0.01. In the absence of fish, smaller individuals appeared to have better body conditions than larger individuals. This trend was little impacted by the amount of fine sediment. However, when fish were present the relationship between body condition and SVL depended on the sediment load (Figure 2): when sediments loads were low, body condition declined with SVL; as sediment loads increased, body condition increased with SVL. Ninety-five percent confidence intervals for coefficients of additional terms present in competing habitat/biotic models overlapped 0. No model from the crossing type candidate model set explained the variation in body condition better than the top habitat/biotic model (Table 4). Further, all 95% confidence intervals for term coefficients in the crossing type candidate model set overlapped 0. Further analyses confirmed that model selection was not biased by unequal ranges of SVL between regions. Finally, individuals with higher body conditions had higher rates of growth (simple linear regression: $p <$ 0.01).

Movement

I recaptured 262 individual *D. aterrimus* at least once, resulting in 262 measurements of net in-reach movement (Figure 3). When pooled across all streams, the distribution of net in-reach movements was left-skewed, indicating more individuals moved downstream than upstream (D'Agostino test: skew = -1.29, $p < 0.01$). The data also had a leptokurtic distribution, indicating that the distribution of net in-reach movements had a wide boundary relative to a normal distribution (Anscombe-Glynn test: kurtosis = 7.43, $p < 0.01$). The longest downstream and upstream net in-reach movements were 61 and 38 m, respectively. The most frequently observed net in-reach movement was 0 m. Individuals were recaptured between one and five times, once being the most common. There was no relationship between the number of times an individual was recaptured and net movements (simple linear regression: $p = 0.20$).

Data describing whether individuals moved or stayed were not overdispersed (resid. dev. / rdf = 1.06). A model including the term fish and a model with only random intercept effects ranked equally to explain whether individuals moved or stayed (Table 5, Table 6). However, the 95% CI for the coefficient for the term for fish overlapped 0. Therefore, I selected the random intercept model as the habitat/biotic model. Including models from the crossing type candidate data set did not improve model fit and 95% CI for all coefficient estimates in these models overlapped 0.

Data describing whether individuals moved downstream or upstream were not overdispersed (resid. dev. / rdf = 1.10). Whether individuals moved upstream or downstream was best explained by the model containing SVL (Table 5, Table 7), where larger individuals were more likely to move upstream and smaller individuals were more likely to move downstream. Including models from the crossing type candidate data set did not improve model fit and 95% CI for all coefficient estimates in these models overlapped 0.

Survival

AIC_c weights indicated that a model structure where recapture probability varied by time and SVL was most parsimonious, where smaller individuals were more likely to be captured than larger individuals (Table 8). This model was approximately 3.8 times more likely than the next highest ranking model, which included an interaction between time and SVL.

The monthly mean apparent survival of *D. aterrimus* across all study reaches was 0.93 (95% credible interval = 0.90 - 0.95) (Table 9). Ninety-five percent credible intervals for apparent survival of individuals in streams with roads and without roads overlapped (Figure 4), as did credible intervals for apparent survival among crossing types (Figure 5). Credible intervals for apparent survival of individuals in upstream and downstream reaches of streams of all crossing types widely overlapped (Figure 6). The estimate of apparent survival in reaches below improved culverts was uninformative.

DISCUSSION

I found no evidence culverts affected in-stream habitat conditions, dispersal of *D. aterrimus*, or biological responses of *D. aterrimus*. Specifically, the amount of fine sediment in reaches downstream of culverts – whether improved or unimproved – was no higher than in other reaches, suggesting that culverts did not affect the habitat conditions that I measured. Also, I did not detect any dispersal events from downstream to upstream reaches in any of my study streams, and, therefore, I was not able to determine whether culverts limit the dispersal of *D. aterrimus* from downstream to upstream reaches. Finally, I found body condition, in-reach movement behavior, and monthly apparent survival of *D. aterrimus* did not vary among the reach types in my study.

Variation of habitat attributes among streams by crossing type did not appear to be a result of culverts or culvert types, but this variation is indicative of current prioritizations for culvert replacement. First, I found that culverts did not cause changes to sediment in reaches downstream of culverts. Though the culverts in my study streams may not have affected sediment loads, additional controls on sedimentation that I did not account for in my models (e.g., drainage area, local geology, fire history, and other land management features) may have influenced the results. Additionally, the amount sedimentation increases due to culverts could vary over time, where the most acute sedimentation occurs during and after culvert installation, and then declines as time passes. Second, other local habitat conditions in my study streams varied by crossing type. Specifically, streams with improved culverts were wider and less steep than streams with unimproved culverts or no culverts. These differences were expected because land managers generally prioritize culvert improvements to benefit fish populations, focusing on

streams lower in watersheds that are relatively wide and less steep. Hence, the current focus of culvert improvement for fish likely has only coincidental benefits for stream amphibians and other stream taxa that generally occupy reaches higher in watersheds (Meyer et al. 2007).

I predicted dispersal of *D. aterrimus* from downstream to upstream reaches would vary by crossing type, where dispersal through unimproved culverts would be less probable than through improved culverts or intervening reaches in streams with no culverts. However, I did not have power to assess this prediction because I did not detect any dispersal events from downstream to upstream reaches in any of the streams I studied. Therefore, whether or not upstream dispersal of *D. aterrimus* is blocked by unimproved culverts, or facilitated by improved culverts, is not clear from my data. Nor are these trends clear from previous research on movements of aquatic *Dicamptodon*, due, in part, to the rarity of such events. Sagar (2004) recorded only two upstream transitions by *D. tenebrosus* larvae through improved culverts and zero through unimproved culverts even though her group marked over 2,000 individuals.

In-reach movement distributions from my data indicate that upstream movements of *D. aterrimus* are less common than downstream movements, and upstream movements are rarely long enough to transition the length of a culvert. Specifically, I detected only two individuals that moved upstream more than 20 m (the mean length of intervening reaches in my study). Therefore, the probability of detecting an upstream dispersal across any of the crossing types in my study was extremely low. Though my study did not show that unimproved culverts with perched outlets block upstream dispersal events of larval and paedomorphic *D. aterrimus*, based on field observations of the swimming abilities of these animals, I believe it logical that these structures do block these events. Future work involving molecular tests for migrant assignment will help to elucidate whether culverts block upstream dispersal events.

Even low rates of upstream dispersal may be important for maintaining populations of *D. aterrimus* in headwater reaches through either demographic or genetic mechanisms (Mills and Allendorf 1996, Lowe 2003), but the importance of these events may depend upon the contribution of terrestrial individuals to population dynamics (Grant et al. 2010). Lowe (2003) found that low levels of dispersal from downstream to upstream reaches by the stream

salamander *Gyrinophilus porphyriticus* provided a demographic benefit to the population in the upstream reach, maintaining equal population growth rates in the reaches despite lower reproduction rates and body conditions of individuals in the upstream reach. In terms of genetic mechanisms, even a single migrant per generation can maintain enough genetic connectivity between populations to prevent negative effects of genetic drift in small populations, though as many ten migrants may be needed in some populations (Mills and Allendorf 1996). A population of fully aquatic organisms in a headwater stream reach will be completely isolated if the only immigrant source – reaches downstream in the stream network – is eliminated due to a barrier in the stream that blocks those movements, such as a perched culvert. For *D. aterrimus*, whose reproductively capable adults include both terrestrial and paedomorphic forms, the importance of in-stream dispersal for maintaining connectivity among populations may be less important than for fully aquatic species, as connectivity among populations could be maintained by overland dispersal pathways in addition to in-stream pathways (Grant et al. 2010). Genetic input via overland pathways may be a mechanism maintaining the nominal biological responses I observed in reaches above unimproved culverts. However, the true contribution from terrestrial morphs to population dynamics (e.g., reproduction) has not been explicitly studied for *D. aterrimus*, and could vary over the species' geographic range (Honeycutt unpublished data).

Even if populations of *D. aterrimus* above unimproved culverts are genetically isolated – in the case that culverts are barriers to upstream dispersal events and terrestrial morphs are not contributing to populations – the effects of isolation on biological responses in those populations may not have been detectable in my study or may be buffered by large effective population sizes. First, numerous empirical studies demonstrate populations experiencing genetic isolation (e.g., Wofford et al. 2005, Epps et al. 2005), however, only recently have examples of fitness related effects of genetic isolation been illustrated (Tallmon et al. 2004). This is because effects of genetic isolation on fitness may be more difficult to detect than genetic signals (Keller and Waller 2002). Therefore, using molecular data to test for genetic drift and inbreeding in potentially isolated populations – such as *D. aterrimus* populations upstream of unimproved culverts – is important for determining their long-term viability, even if those populations do not currently show symptoms of reduced fitness. Also, if isolation from culverts does affect the apparent survival of *D. aterrimus,* a higher number of reach replicates may be necessary to

statistically resolve these effects. In my study, the estimate of apparent survival for each crossing type was based on six replicates, while this estimate for each reach type was based on only three replicates. From these data I found variation in monthly apparent survival among crossing types resolved to reasonable credible intervals, but the resolution of those intervals among reach types was quite low. Second, large effective genetic sizes may buffer effects of isolation that lead to fitness deficits (Newman and Pilson 1997). In my study, habitat patches continuous with reaches above culverts may be large enough, and may contain enough *D. aterrimus* individuals, to maintain large effective genetic sizes. If this is true, populations of *D. aterrimus* above culverts could sustain nominal biological responses without genetic maintenance by migrants from downstream reaches (Prugh et al. 2008).

D. aterrimus may be tolerable of a range of local habitat conditions (Welsh and Ollivier 1998, Sepulveda and Lowe 2009), and, therefore, their demographic rates may not be strongly responsive to variation in sedimentation, except under specific circumstances. Though increased sedimentation is expected to negatively affect organisms across taxa (Henley et al. 2000), including stream breeding amphibians (Corn and Bury 1989, Gillespie 2002), two studies have found no negative effects of increased sediment on demographic rates of *Dicamptodon* species (Welsh and Ollivier 1998, Sepulveda and Lowe 2009). In my study, body condition, in-reach movement behavior, and survival of *D. aterrimus* did not vary among the reach types. However, the body condition of *D. aterrimus* did change in response to local habitat variation among the study streams, although these habitat conditions were not directly influenced by culverts. The highest ranked model explaining body condition included the interaction among sediment load, fish presence, and individual size. Specifically, in the absence of fish, smaller individuals appeared to have better body conditions than larger individuals and the amount of fine sediment did little to affect this trend. However, when fish were present the relationship between body condition and SVL depended on the sediment load: when sediment loads were low, body condition declined with SVL; as sediment loads increased, body condition increased with SVL. The availability of interstitial refuges may explain these effects. When fish are present and sediment loads are low, small salamanders likely feed within spaces among cobles and boulders, perhaps avoiding stressful interactions with fish (Sih et al. 1992). However, when fine sediments are high, these interstitial spaces are filled. In the presence of fish and high sediment loads, the

ability of individuals to hide and rest is likely diminished, reducing foraging efficiency (Semlitsch 1987). Though sedimentation and fish effects were not consistently associated with culverts and reach positions, my data suggest that in cases where roads and unimproved culverts do increase sediment loads in streams (Rice 1999), this could affect the body condition of smaller size *D. aterrimus* where fish are present. This indicates that although *D. aterrimus* may be habitat generalists, and do not in general respond negatively to increased sediment loads (Sepulveda 2009, Welsh 1998), the effects of sediment on this species may depend on life stage and community dynamics (Gillespie 2002).

In-reach movements of *D. aterrimus* were not affected by culverts; however, measures of *D. aterrimus* movement varied by size. My results indicate that larger salamanders were more likely to move upstream than downstream. This result is consistent with work by Sepulveda and Lowe (2011) where, in a pair of streams, *D. aterrimus* that moved upstream were larger than those that moved downstream. This indicates that individual size may be a predictor of movement direction, with the probability of moving upstream increasing as individuals grow. If this is true, individuals might move downstream during their initial life stages, then return upstream during later life stages. A similar trend was detected by Bruce (1986), who found that first-year larvae of two-lined salamanders represented a larger proportion of individuals moving in a downstream direction than second-year larvae, but that the proportions of first- and second-year larvae moving upstream were similar. Therefore, the potential effects of culverts on upstream movements by *D. aterrimus* could vary by individual size, and unimproved culverts have the potential to block upstream movements of breeding-age *D. aterrimus*.

My study did not show that culverts affect the biological responses of *D. aterrimus* that I measured. However, because of the high potential for these structures to isolate populations of *D. aterrimus*, there are several issues managers and researchers might address to ensure the viability of populations above unimproved culverts into the future. Because multiple dispersal pathways can facilitate population persistence in headwater streams (Grant et al. 2010), determining patterns in the proportions of terrestrial and paedomorphic adult *D. aterrimus* within populations, and whether *D. aterrimus* utilize multiple dispersal pathways, will be important to guiding management of this species. Likewise, assessing spatial variation of the contribution of terrestrial

morphs to the demographic and genetic properties of populations could be important for determining whether in-stream barriers to upstream *D. aterrimus* dispersal are important at the population level. Also, using molecular techniques to detect signals of population connectivity may be more advantageous than using CMR techniques to detect rare dispersal events. Until questions regarding terrestrial contribution are resolved, broadening the scope of culvert improvements to include aquatic species other than fish and culverts higher in watershed would likely benefit *D. aterrimus.*

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Table 1. AIC_c rankings of habitat models explaining the amount of fine sediments measured in the nine study streams. All models include stream as a random intercept; this is the only term included in the model named *Only Random Effects.* Region indicates whether a stream was in the northern or southern region of the study area, width is the natural log of wetted width, pool is the natural log of percent pool coverage, and gradient is the natural log of stream gradient calculated as a proportion. *K* is the number of parameters in the model.

Model Structure	***K***	**log Likelihood**	**AIC_c**	**ΔAIC_c**	**Weight**	**Model Likelihood**
Region + Width + Pool	6	143.4	-274.2	0	0.360	1
Region + Pool	5	142.3	-274.1	0.1	0.340	0.944
Region + Width + Gradient + Pool	7	143.4	-272.1	2.1	0.120	0.333
Width + Pool	5	141.1	-271.8	2.4	0.110	0.306
Pool	4	139.6	-270.9	3.3	0.070	0.194
Region + Width	5	136.3	-262.2	12.0	< 0.001	< 0.003
Width	4	134.7	-261.2	13.0	< 0.001	< 0.003
Region	4	133.9	-259.5	14.8	< 0.001	< 0.003
Only Random Effects	3	131.8	-257.5	16.7	< 0.001	< 0.003

Table 2. AIC_c rankings of models from the crossing type candidate set explaining the amount of fine sediments measured in the nine study streams, after accounting for the habitat parameters of region and pool. All models include stream as a random intercept. Region indicates whether a stream was in the northern or southern region of the study area, pool is the natural log of percent pool coverage, road is whether or not a road was present at a stream, type is crossing type, and reach is reach position. *K* is the number of parameters in the model.

Model Structure	***K***	**log Likelihood**	**AIC_c**	**ΔAIC_c**	**Weight**	**Model Likelihood**
Region + Pool	5	142.3	-274.1	0	0.404	1
Road + Region + Pool	6	143.1	-273.6	0.5	0.311	0.770
Type + Region + Pool	7	143.8	-272.8	1.3	0.208	0.515
Road × Reach + Region + Pool	8	143.7	-270.3	3.8	0.061	0.151
Type × Reach + Region + Pool	10	144.7	-267.8	6.4	0.017	0.042

Table 3. AIC_c rankings of habitat/biotic models explaining the body condition of individuals measured at the time of initial capture in the nine study streams. All models include stream as a random intercept; this is the only term included in the model named *Only Random Effects.* SVL is the natural log of SVL, width is the natural log of wetted width, pool is percent pool coverage, fine is percent fine sediments, and fish represents whether or not fish were present. *K* is the number of parameters in the model.

Model Structure	*K*	log Likelihood	AIC_c	ΔAIC_c	Weight	Model Likelihood
SVL × Fine × Fish + Region	11	-1507.1	3036.4	0	0.365	1
SVL × Fine × Fish + Region + Pool	12	-1506.6	3037.5	1.0	0.217	0.595
SVL × Fine × Fish + Region + Width	12	-1506.9	3038.2	1.8	0.149	0.408
SVL × Fine × Fish + Region × SVL	12	-1506.9	3038.2	1.7	0.153	0.419
SVL × Fine × Fish + Region + Pool + Width	13	-1506.5	3039.4	3.0	0.081	0.222
SVL × Fine × Fish + Region × SVL + Pool + Width	14	-1506.4	3041.2	4.8	0.033	0.090
SVL × Fine + SVL × Fish + Region	9	-1515.1	3048.4	12.0	< 0.001	< 0.003
SVL × Fish + Fine + Region	8	-1517.8	3051.8	15.4	< 0.001	< 0.003
SVL × Fish + Fine × Fish + Region	9	-1517.8	3053.8	17.4	< 0.001	< 0.003
SVL × Fish + Region	7	-1520.1	3054.4	18.0	< 0.001	< 0.003
SVL × Fine × Fish	10	-1519.1	3058.5	22.0	< 0.001	< 0.003
SVL × Fine + Fine × Fish + Region	9	-1521.5	3061.2	24.7	< 0.001	< 0.003
SVL + Fine + Region	6	-1526.2	3064.4	28.0	< 0.001	< 0.003
SVL + Fine + Fish + Region	7	-1526.2	3066.4	30.0	< 0.001	< 0.003
SVL + Fine × Fish + Region	8	-1526	3068.1	31.7	< 0.001	< 0.003
SVL + Region	5	-1530	3070.2	33.7	< 0.001	< 0.003
Region	4	-1547.3	3102.6	66.2	< 0.001	< 0.003
Fine + Fish + Region	6	-1545.9	3103.9	67.5	< 0.001	< 0.003
Only Random Effects	3	-1553.2	3112.5	76.1	< 0.001	< 0.003

Table 4. AIC_c rankings of models from the crossing type candidate set explaining the body condition of individuals measured at the time of initial capture in the nine study streams, after accounting for the habitat/biotic parameters of SVL × Fine × Fish + Region (SFF+R). All models include stream as a random intercept. Road is whether or not a road was present at a stream, type is crossing type, and reach is reach position. Region indicates whether a stream was in the northern or southern region of the study area, SVL is the natural log of SVL, fine is percent fine sediments, and fish represents whether or not fish were present. *K* is the number of parameters in the model.

Model Structure	*K*	log Likelihood	AIC_c	ΔAIC_c	Weight	Model Likelihood
SFF+R	11	-1507.1	3036.4	0	0.574	1
Road + SFF+R	12	-1507.1	3038.5	2.0	0.207	0.361
Road × Reach + SFF+R	14	-1505.6	3039.7	3.3	0.112	0.195
Type + SFF+R	13	-1506.9	3040.2	3.8	0.085	0.148
Type × Reach + SFF+R	16	-1505.2	3042.9	6.5	0.022	0.038

Table 5. AIC_c rankings of habitat/biotic models explaining the movements of individuals measured over two years in the nine study streams. The results for two aspects of movement are given in the table: 1) whether individuals moved or stayed and 2) whether individuals moved in an upstream or downstream direction. All models include stream as a random intercept; this is the only term included in the model named *Only Random Effects.* Only the four highest ranking models are given for each test. SVL is the natural log of SVL, fish represents whether or not fish were present, region indicates whether a stream was in the northern or southern region of the study area, and gradient is the natural log of stream gradient calculated as a proportion. *K* is the number of parameters in the model.

Test	Model Structure	*K*	log Likelihood	AIC_c	ΔAIC_c	Weight	Model Likelihood
Move / Stay	Fish	3	-142.2	290.5	0	0.165	1
	Only Random Effects	2	-143.2	290.5	0	0.165	1
	SVL + Fish	4	-142	292.1	1.6	0.076	0.461
	Fish + Region	4	-142	292.2	1.7	0.071	0.430
Up / Down	SVL	3	-113	232.2	0	0.329	1.000
	SVL + Region	4	-112.7	233.5	1.4	0.165	0.501
	SVL + Fish	4	-112.9	234.1	1.9	0.126	0.383
	SVL + Gradient	4	-113	234.2	2.0	0.121	0.367

Table 6. AIC_c rankings of models from the crossing type candidate set explaining whether individuals moved or stayed, as measured over two years in the nine study streams. A model including only random intercept effects of stream represented the top habitat/biotic model. All models include stream as a random intercept. Road is whether or not a road was present at a stream, type is crossing type, and reach is reach position. *K* is the number of parameters in the model.

Model Structure	*K*	log Likelihood	AIC_c	ΔAIC_c	Weight	Model Likelihood
Only Random Effects	2	-143.2	290.5	0	0.543	1
Type	4	-142.2	292.6	2.0	0.196	0.361
Road	3	-143.2	292.6	2.0	0.196	0.361
Road × Reach	5	-142.6	295.4	4.9	0.048	0.088
Type × Reach	7	-141.5	297.4	6.9	0.017	0.031

Table 7. AIC_c rankings of models from the crossing type candidate set explaining whether individuals moved up or down, as measured over two years in the nine study streams. Each model contains the structure of the top model from the selection of the habitat/biotic parameters (SVL). All models also include stream as a random intercept. SVL is the natural log of SVL, road is whether or not a road was present at a stream, type is crossing type, and reach is reach position. *K* is the number of parameters in the model.

Model Structure	*K*	log Likelihood	AIC_c	ΔAIC_c	Weight	Model Likelihood
SVL	3	-113	232.2	0	0.500	1
SVL + Road	4	-112.5	233.2	1.0	0.296	0.592
SVL + Type	5	-112.4	235.2	3.0	0.109	0.218
SVL + Road × Reach	6	-111.9	236.2	4.0	0.067	0.134
SVL + Type × Reach	8	-110.6	237.9	5.7	0.028	0.056

Table 8. AIC_c rankings for model structures explaining recapture probability (p) of individual *D. aterrimus* captured over two years in the nine study streams. Initial position is the initial location in the reach where an individual was captured, effort is the number of seconds spent electrofishing, and time allows for p to vary among primary capture sessions. A parameter explaining apparent survival for each reach is included in each model, accounting for 18 parameters per model. K is the total number of parameters in the model.

Model	K	Deviance	AIC_c	ΔAIC_c	Weight	Model Likelihood
p(time + SVL)	25	1333.01	1384.4	0	0.781	1
p(time × SVL)	31	1322.91	1387.1	2.7	0.205	0.262
p(time)	24	1343.77	1393.1	8.7	0.010	0.013
p(time + Initial Position)	25	1343.34	1394.8	10.3	0.004	0.006
p(time × Stream)	62	1286.88	1419.9	35.5	< 0.001	< 0.003
p(Effort)	20	1385.21	1426.1	41.7	< 0.001	< 0.003
p(Effort + Reach)	37	1349.96	1427.1	42.7	< 0.001	< 0.003
p(Effort × Reach)	55	1317.78	1434.8	50.4	< 0.001	< 0.003
p(SVL)	20	1402.22	1443.1	58.7	< 0.001	< 0.003
p(.)	19	1410.94	1449.8	65.3	< 0.001	< 0.003
p(Stream)	27	1396.06	1451.7	67.3	< 0.001	< 0.003
p(Reach)	36	1376.94	1451.9	67.5	< 0.001	< 0.003
p(time × Reach)	106	1232.62	1472.2	87.7	< 0.001	< 0.003

Table 9. Apparent survival estimates from CMR surveys over two years in the nine study streams. The mean and standard deviation (std dev) are given for the hyperdistributions of the *beta* parameters. The means of the real parameters, derived from the logit-link function of the *beta* parameters, are also given along with 95% credible intervals. N represents the number of reaches included in each hyperdistribution.

		***Beta* Parameters**		**Real Parameters**		
Reach Type	**n**	**Mean**	**Std dev**	**Mean**	**2.5%**	**97.5%**
All Streams	18	2.541	0.176	0.927	0.903	0.949
No Roads	6	2.702	0.345	0.937	0.894	0.970
Roads	12	2.546	0.208	0.927	0.898	0.952
No Culvert	6	2.718	0.350	0.935	0.896	0.970
Improved	6	2.663	0.470	0.929	0.869	0.978
Unimproved	6	2.566	0.322	0.926	0.887	0.965
No Culvert Down	3	3.143	1.4915	0.959	0.634	0.999
No Culvert Up	3	2.652	0.9097	0.934	0.798	0.987
Improved Down	3	2.807	2.4239	0.943	0.073	1.000
Improved Up	3	2.905	1.4025	0.948	0.751	0.998
Unimproved Down	3	2.910	0.6460	0.948	0.890	0.985
Unimproved Up	3	2.313	0.7393	0.910	0.766	0.977

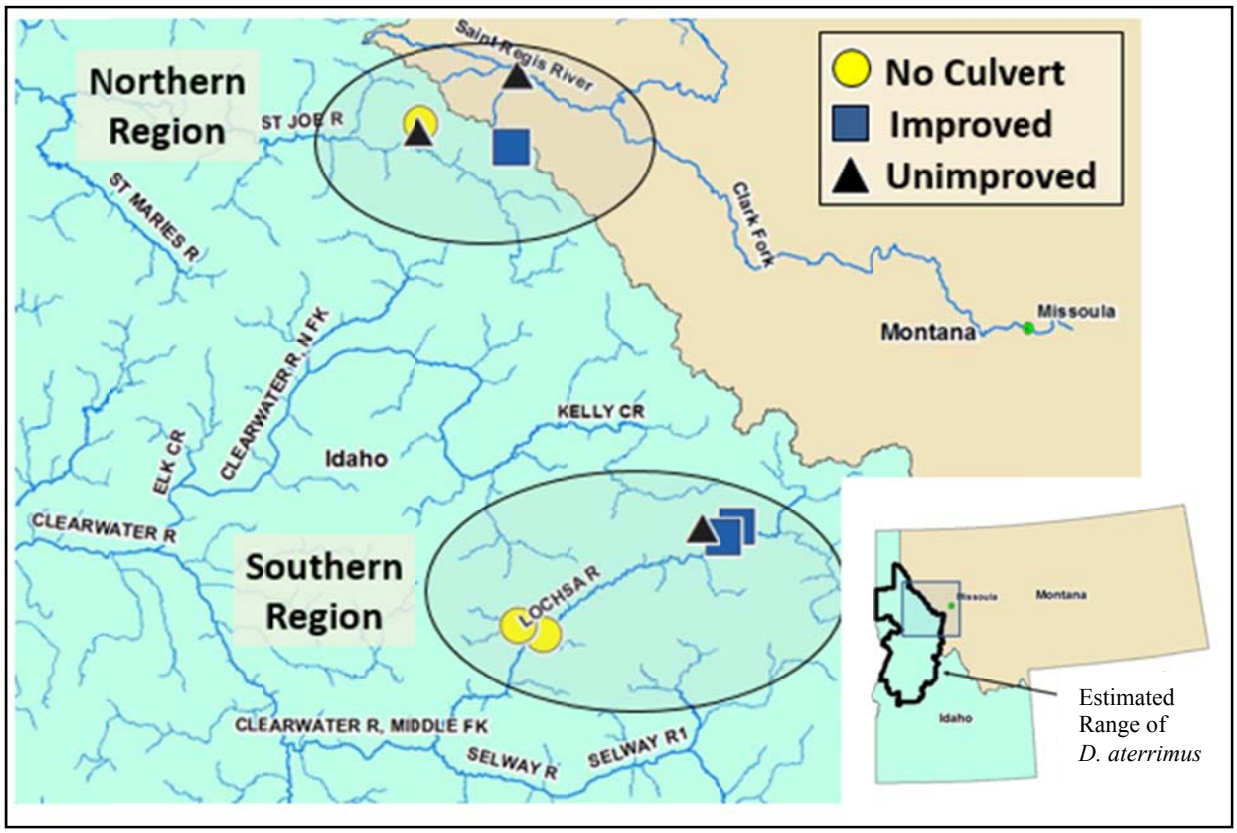
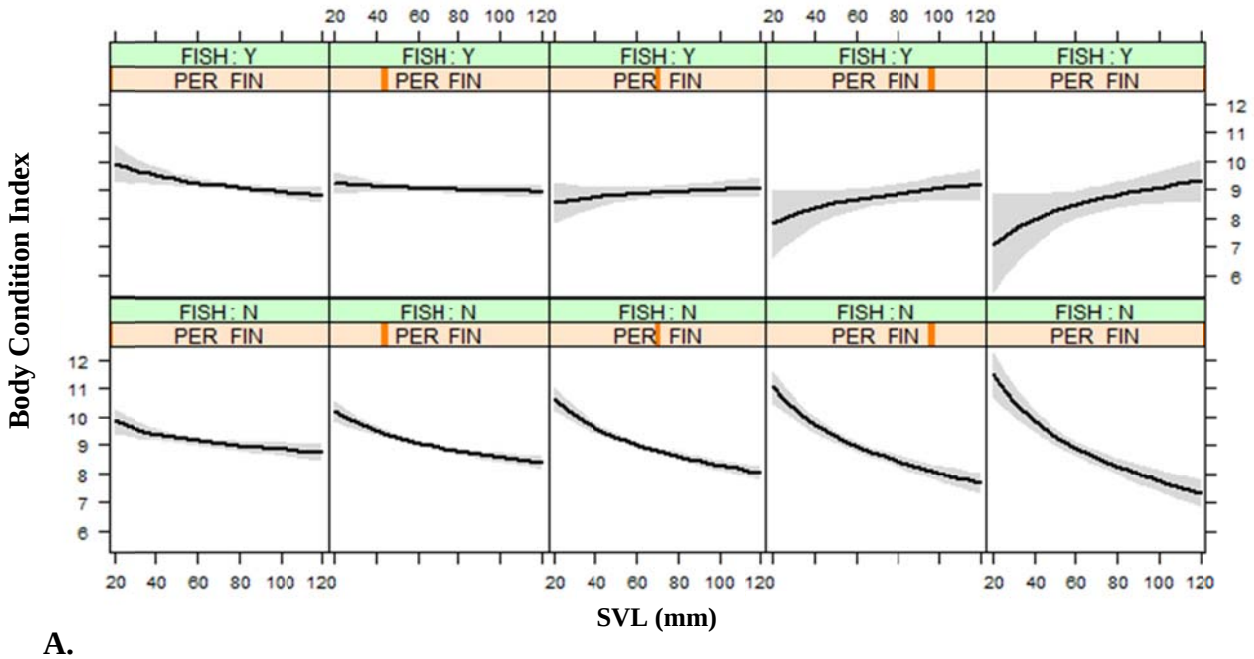
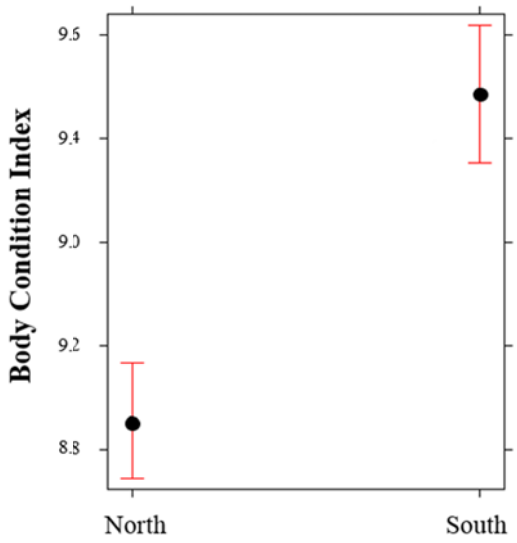


Figure 1. The locations of my study streams. The small inset map shows the broader geographic region surrounding the study area and the estimated range of *D. aterrimus* delineated with the bold black polygon. The location of the enlarged map is delineated by the square in the inset map.



A.



B.

Figure 2. The predicted effects from the model for body condition containing SVL × Fine × Fish + Region. In *Figure A*, the x-axis for each panel represents SVL. The bottom row of panels indicates the prediction when fish are absent and the top row when fish are present. The percent fine sediments (PER_FIN) increases from left to right among the panels in each row. Figure *B* provides the estimated regional effects on body condition.

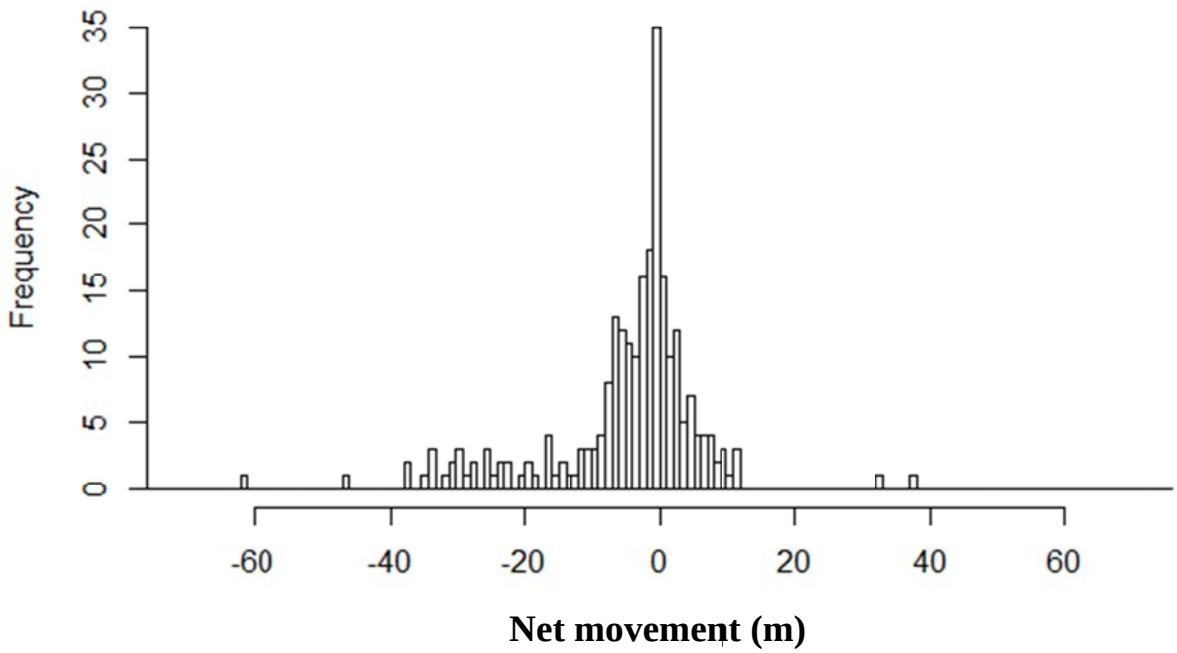


Figure 3. The distribution of in-reach net movements of *D. aterrimus* pooled across all streams. Negative values indicate downstream movements and positive values indicate upstream movements.

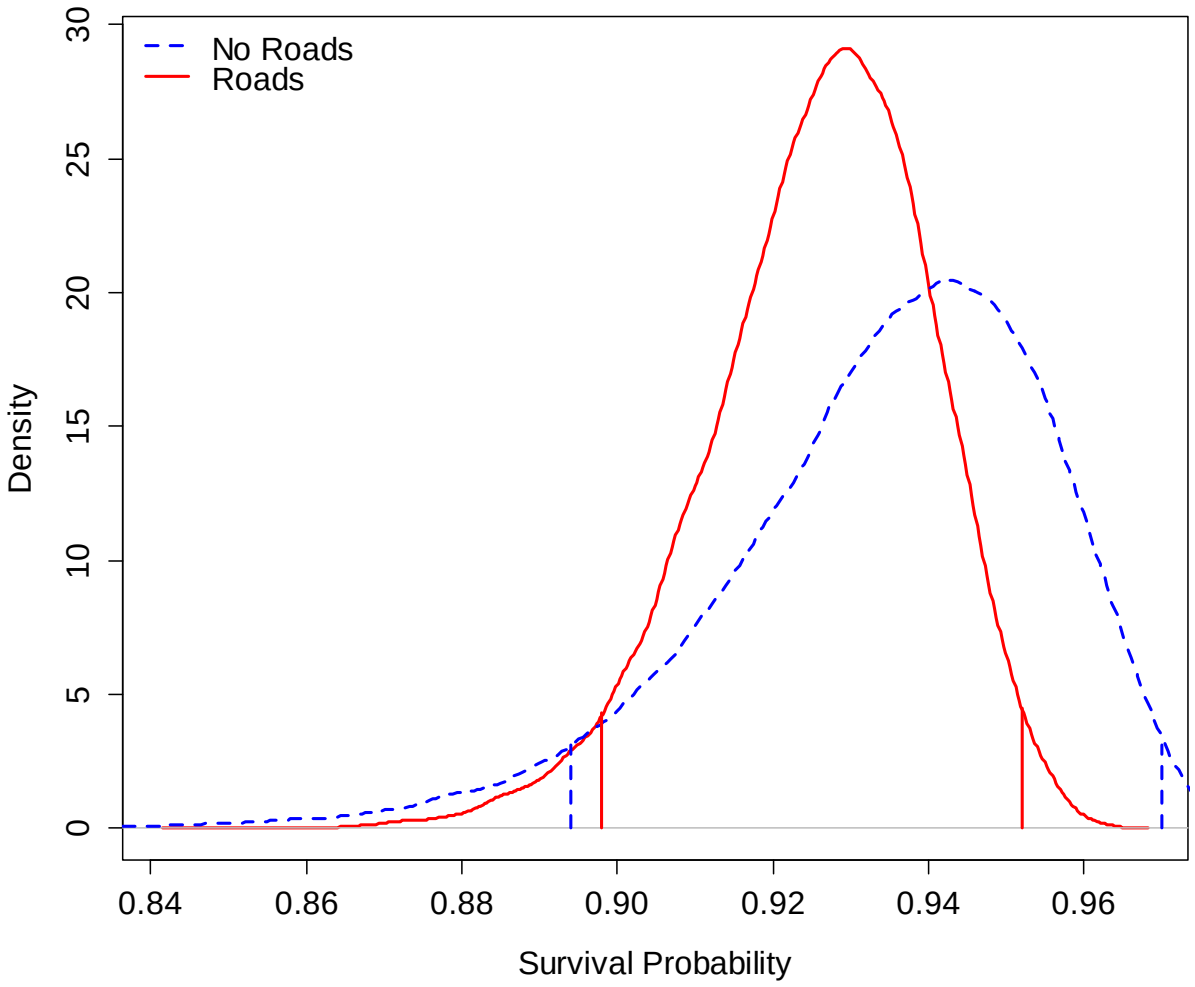


Figure 4. The density of the posterior distribution of monthly survival probability for *D. aterrimus* in reaches adjacent to roads (n = 12) vs reaches not adjacent to roads (n = 6). The density curves represent random draws of 10,000 samples from a normal distribution with means and standard deviations equal to the means and standard deviations of the posterior distributions for each reach type. The vertical lines represent 95% credible intervals.

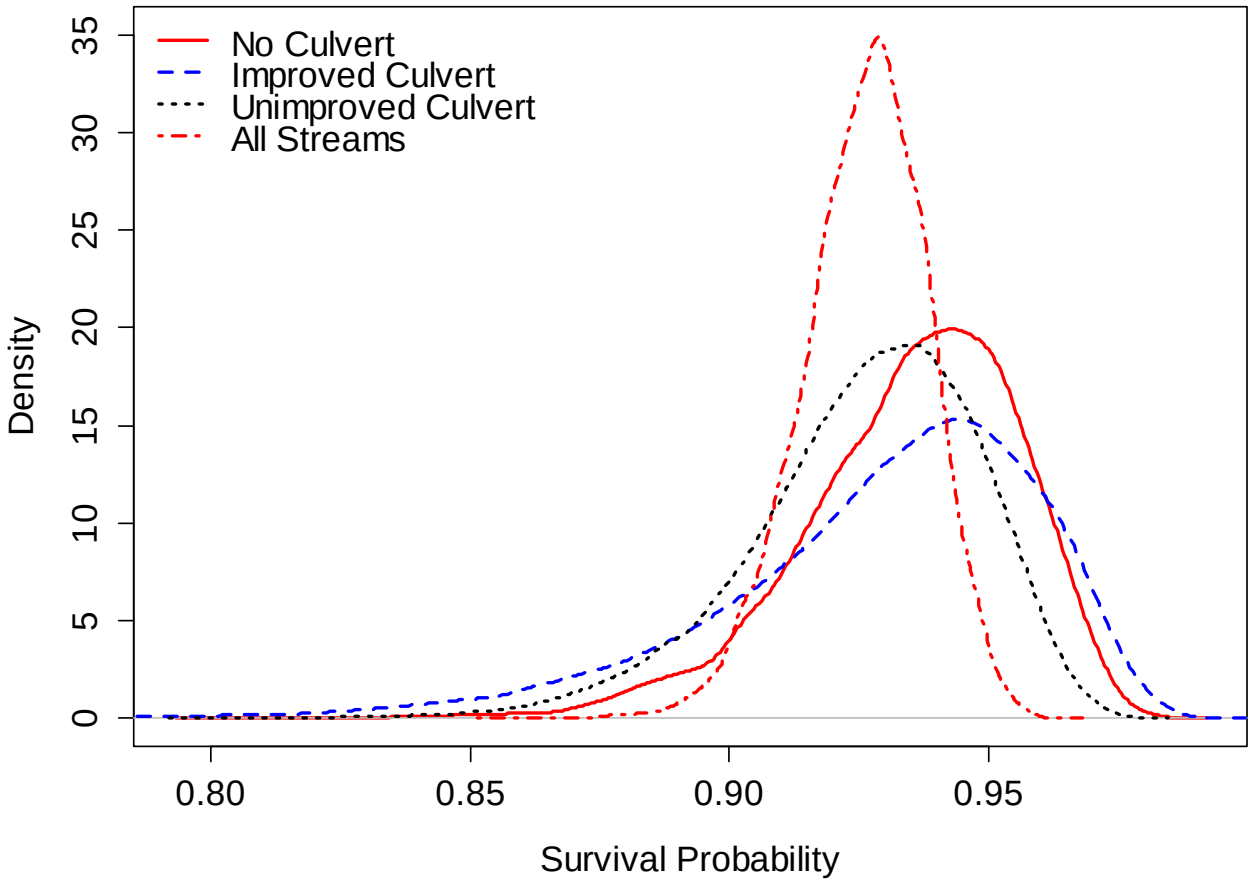


Figure 5. The density of the posterior distribution of monthly survival probability for *D. aterrimus* in all stream types. The density curves represent random draws of 10,000 samples from a normal distribution with means and standard deviations equal to the means and standard deviations of the posterior distributions for each crossing type – or for all streams – when that is the case.

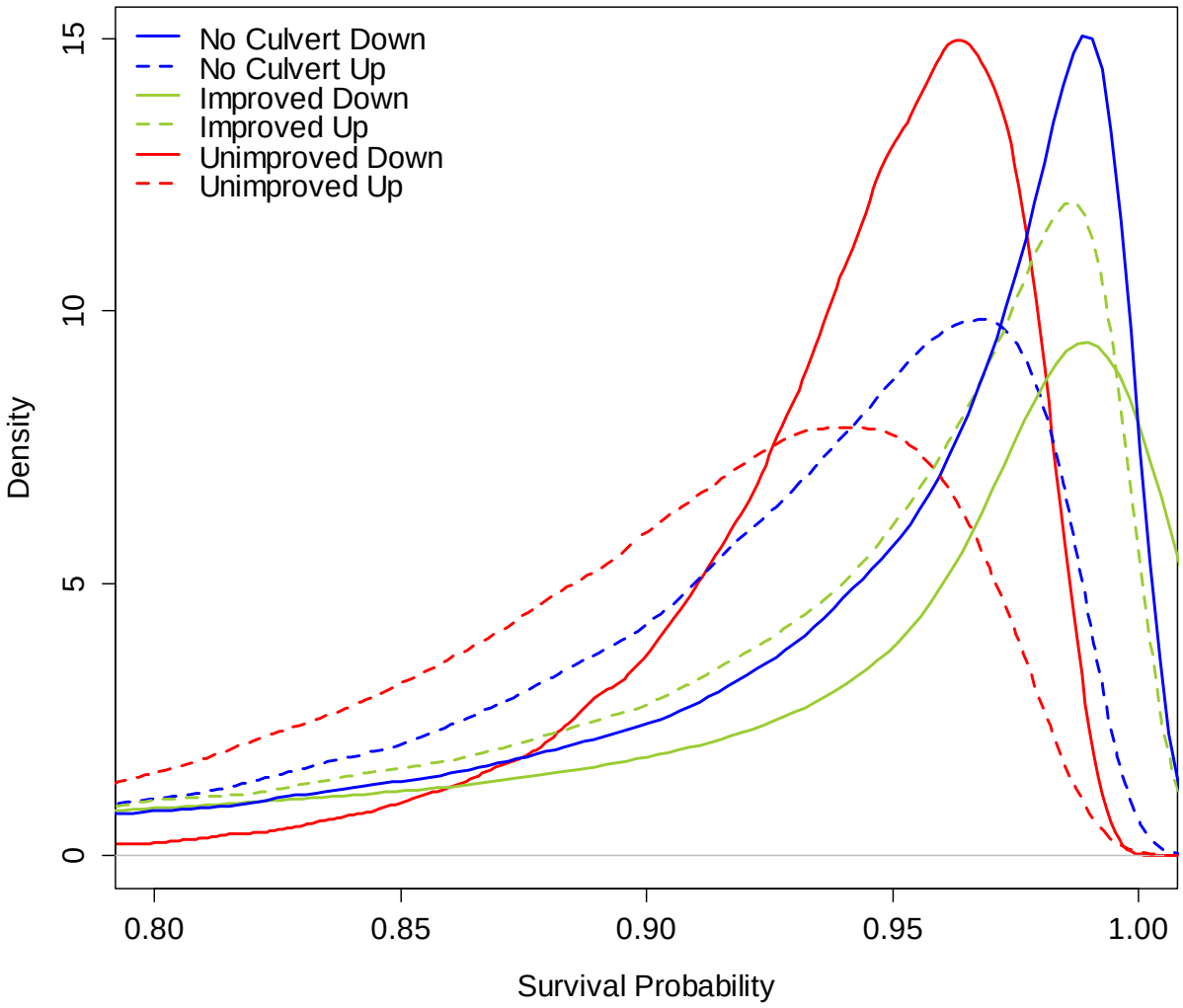


Figure 6. The density of the posterior distribution of monthly survival probability for *D. aterrimus* in reaches for all reach types. The density curves represent random draws of 10,000 samples from a normal distribution with means and standard deviations equal to the means and standard deviations of the posterior distributions for each reach type.

APPENDIX

Appendix 1 – Approach to study stream selection

To select the nine study streams, I first compiled a database of all known locations where streams are bisected by culverts within the range of *D. aterrimus*. I created this database from USFS records, maps, and local expert knowledge. I used a geographical information system to limit the results in this database to 1st and 2nd order streams, as it is believed that *D. aterrimus* are more detectable or occur more frequently in these streams than in larger streams (Sepulveda and Lowe 2009). Because I hypothesized that unimproved culverts that are barriers to fish movement may also be barriers to *D. aterrimus* movement, I further limited the population of possible unimproved culverts with information from Hendrickson et al. (2008), which assessed the barrier potential of individual culverts to fish passage. I limited the population of culverts to those flagged by Hendrickson et al. (2008) as possible or potential barriers to fish movement and to culverts recently replaced to mitigate fish passage. To broaden the range of potential study streams containing improved culverts, I also included culverts flagged as arch style and natural bottom. I then field checked these culvert locations to assess culvert type and relative *D. aterrimus* abundance in the adjoining stream reaches.

From information gained about the physical characteristics of culverts during my field assessment, I assigned culverts into two categories: improved and unimproved. Improved culverts were designed by engineers to meet a specific need (i.e., to facilitate fish passage), so can be defined with a relatively narrow scope of characteristics. Improved culverts had a simulated natural stream bottom throughout the length of the culvert, a gradient similar to the streams they bisect, outlets at stream grade, and width greater than the wetted width of the stream during base flow. Unimproved culverts encompass a wider range of characteristics. However, the culverts in my unimproved category did not have natural substrate throughout the length of the culvert, were narrower than the wetted width of the streams during base flow, and generally had perched outlets that were above the grade of the streams.

To assess relative *D. aterrimus* abundance within potential study reaches, I surveyed approximately 25 m of stream contiguously below and above each culvert using a Smith-Root

LR-24 backpack electrofishing unit and a capture net. I recorded naïve abundance and I accounted for search effort by recording the number of seconds spent electrofishing. I defined relative abundance among streams as the number of salamanders observed divided by the seconds spent electrofishing. In total, I searched for *D. aterrimus* in 147 stream segments. In addition to surveys in streams bisected by culverts, I assessed relative *D. aterrimus* abundance in several 1st and 2nd order streams without culverts.

From this population of streams initially surveyed, I selected my nine survey streams based on *D. aterrimus* abundance and physical attributes of culverts. Because inference from CMR studies is often limited by low numbers of individuals, I first ranked the potential streams by salamander abundance. I then examined the physical attributes of culverts in streams where salamander abundance was highest. As my goal was to measure the effect of different crossing types on body condition, in-reach movement, and survival of *D. aterrimus*, I ranked streams based on the physical attributes of the culverts that bisected them. I ranked improved culverts by how rigidly they fit my definition of an improved culvert. I ranked unimproved culverts by a qualitative assessment of the following attributes: the height from the outlet of the culvert to the water below, the steepness of the culvert gradient relative to the gradient of the stream, the amount of natural substrate contained in the culvert, and the ratio of the width of the culvert to the wetted width of the stream. I gave higher rankings to unimproved culverts with higher outlet drops, steeper gradients, low amounts of natural substrate, and which were narrow relative to the stream they carried. I also gave higher rankings to unimproved culverts which I thought would most likely be barriers to the movement of larval and paedomorphic *D. aterrimus*. Finally, I considered logistical concerns related to repeated sampling of nine locations during the short Northern Rocky Mountain summer. The attributes of these streams and associated culverts are summarized in Appendix 2. Study reaches in reference streams were delineated such that the lower end of each downstream reach was at least 30 m above the closest downstream confluence.

Appendix 2. The stream names, their associated crossing types, and the regions the streams were located in. The table also indicates the number of primary survey periods conducted at each stream.

Stream	Type	Region	Primary Periods
Lone Knob	Reference	South	6
Pagoda	Reference	South	6
Bird-2	Reference	North	6
Bird-1	Unimproved	North	6
Mayo	Unimproved	North	6
Waw'aalamnime	Unimproved	South	6
Float	Improved	North	5
Badger	Improved	South	6
Wendover	Improved	South	6